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notes ineffective. I also constructed diapason pipes over 60 cm. long and 5 cm. in diameter, which were excited with my adjustable embouchure. The full c' obtained had the same direct effect on the interferometer as the clarionette. This discrepancy is exceedingly difficult to eliminate as it calls for a detection of the resonant member of the interferometer.

With the 1-foot diapason organ pipes used above, there is much less danger of direct influence. This is shown, for instance, in the balance obtained with nodes of opposite sign. Moreover, I made control experiments by blowing equipitched diapason pipes strongly in the neighborhood. There is even here liable to be a little response. The tendency to assume wave form may be recognized; but it is much smaller than the pipe note proper, and quite absent in the overtones. Finally, the elbowed pipe, figure 3, which blows away from the interferometer, was used for additional guarantee and for overtone nodes.

A PRELIMINARY NOTE ON THE RESULTS OF CROSSING CERTAIN VARIETIES OF NICOTIANA TABACUM

By William Albert Setchell, Thomas Harper Goodspeed and Roy Elwood Clausen

Department of Botany and Division of Genetics of the Department of Agriculture, University of California

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In connection with a taxonomic study of the various species and varieties of *Nicotiana*, the authors became interested in the extremely varied assemblage of varieties, both botanical and commercial, included under the species *N. Tabacum*. The senior author ventured to suggest a preference for five type varieties as representative of the range of variation found within the species and possibly of fundamental importance as stem forms in the derivation of other varieties. A similar attempt to refer existing commercial varieties to derivation from a limited number of fundamental forms had previously been made both by Comes[1] and Anastasia.[2] These authors agreed in principle on the method of derivation of existing varieties, but they held conflicting views as to which particular forms should be recognized as fundamental. In all three cases the principle followed in attempting to unravel the problem of origin of cultivated forms was to determine which few historically old varieties possessed in various combinations all the characters exhibited by commercial varieties, and then to refer existing varieties to hybridization with resulting segregation and recombination of characters exhibited in the stem forms.

The senior author, having tentatively selected five such stem forms, thought it wise by actual genetic experimentation to determine what results would follow hybridization among them. The authors also found themselves in need of some definite information as to the Mendelian details involved in character differences within the species. Accordingly three crosses were actually made and studied at some length. In some cases derivative lines were carried into the tenth hybrid generation. The three crosses, all in reciprocal, were made in 1909 as follows: (1) *angustifolia x macrophylla,* (2) *calycina x virginica* (Maryland) and (3) *alba* (White) *x macrophylla.* Detailed descriptions of the above-named varieties have been given by Setchell[3] in a previous paper. In this article we shall confine our attention to the Mendelian results of the studies.

The Angustifolia-Macrophylla Series.—In the *angustifolia-macrophylla* series an attempt was made to subject two character differences to Mendelian analysis, viz., the light pink flower color of *angustifolia* versus the red of *macrophylla* and the long-petioled leaf-base of *angustifolia* versus the sessile, broad leaf-base of *macrophylla.* The former of these contrasts proved to be a simple monogenic one, but the latter necessitated a complex Mendelian formulation.

Turning our attention to flower color first, F_1 was pink-flowering but the intensity of coloration was distinctly greater than that of *angustifolia.* Ten F_2 families containing a total of 490 plants consisted of 377 pink-flowering and 113 red-flowering plants. The pink-flowering segregants clearly gave evidence of the existence of two sub-classes differing in intensity of coloration. The count totalled 240 pink-flowering and 137 light pink-flowering individuals, a rough approximation to a 2 : 1 ratio. Very little reliance, however, can be placed upon this classification because of the evident intergrading of the two sub-classes. Separation into red and pink was clear and distinct. The F_3 populations conformed to expectation based upon the F_2 results, with the single exception noted below. Four F_2 red-flowering selections gave 99 F_3 plants all red-flowering. Of fifteen F_2 pink-flowering selections ten gave progenies exhibiting segregation in conformance with the 3 pink: 1 red ratio, the actual totals being 187 pink: 60 red. Four F_2 pink-flowering selections bred true for pink, the entire 89 F_3 plants being pink. One population from an F_2 pink-flowering selection yielded a progeny consisting entirely of red-flowering plants. It is difficult to state whether this result indicates a misclassification of the F_2 parent or whether some other experimental error was to blame for it. Taken as a whole the data adequately establish the monogenic nature of the pink : red character contrast. Light pink is to be considered as incompletely dominant over red, and the genetic difference may be designated by the symbols R for light pink and r for red.

The analysis of the leaf-base difference proved to be rather complicated. F_1 was petioled, but the petiole was shorter than that of *angustifolia* and the wing of the petiole was more amply developed. In F_2 a hopelessly complex series of forms was obtained ranging from extremely long-petioled to very broadly sessile types. Although it was impossible to demonstrate any valid Mendelian distribution in F_2, it was possible to distinguish certain forms as centers of distribution. Twenty F_2 selections with respect to the character of the leaf base were made and their progenies were studied in F_3 and subsequent generations. The twenty selections fell into six general leaf types, the names and descriptions of which follow:

1. *Stenophylla*, long-petioled like *angustifolia*, and with a minimum wing development along the petiole.
2. *Latifolia*, short but distinctly petioled like the F_1, and with a variable wing development.
3. *Lanceolata*, broad-based sessile leaves with long lanceolate blades.
4. *Loriifolia*, sessile leaves with very narrow strap-like blades.
5. *Auriculata*, leaves with the blades sharply constricted at the base, nearly if not quite to the mid-rib, and typically with clasping auricles. In some *auriculata* forms the auricles may be absent, in which case the leaf may appear to have a short distinct petiole.
6. *Sessilifolia*, sessile leaves with a broad base and a broad clasping insertion.

Of the above six types of leaves, three, *lanceolata, loriifolia*, and *sessilifolia*, differ merely in width of blade. Genetically they appear to be identical in their leaf-base factors. For the purposes of this discussion, therefore, it is only necessary to distinguish four primarily leaf-base types, *stenophylla, latifolia, sessilifolia*, and *auriculata*.

As we have stated, F_2 gave no decisive evidence either as to the number of factors involved in the leaf-base contrast or as to the interactions among them. In order to obtain suitable analytical material we were obliged to study populations of F_3 and subsequent generations. In such populations a notable simplification was observed in the number of segregation products, and the distribution into classes was more distinct. In the course of the investigations, also, constant derivatives of the various leaf-base types mentioned above were established, and further information as to the genetic relation of the different types was obtained by intercrossing these lines and by crossing them with the original parents. Theoretically such lines should differ less from the parents and from one another than the original parents did from each other, and practically this was found to be the case. The behavior in skeleton of selections of various leaf-base types is given below.

Stenophylla selections were observed to segregate in a variety of ways. Two populations bred true for *stenophylla;* three segregated into 3 *stenophylla:* 1 *sessilifolia;* and one gave 3 *stenophylla:* 1 *auriculata.* A *latifolia* derivative crossed with *angustifolia* gave F_1 *stenophylla*, and F_2 3 *stenophylla:* 1 *latifolia.*

Latifolia selections proved rather perplexing. In some cases *latifolia* is evidently a complex hybrid expression, as is evidenced by the fact that the F_1 cross between the original parents was typically *latifolia* in appearance. One selection repeated the complex F_2 segregation in F_3; two bred true for the *latifolia* leaf-base type; one gave a fairly definite segregation into 3 *latifolia:* 1 *sessilifolia* with subsequent establishment of both types in constant derivative lines; and one population gave 3 *latifolia:* 1 *sessilifolia.*

Sessilifolia selections behaved very simply. Of nine such selections, five bred true for *sessilifolia,* and the remaining four gave 3 *sessilifolia:* 1 *auriculata.*

Auriculata selections appear to breed true whenever tested. One population is an exception to this statement, but it was unfortunately not further investigated. Two other selections bred true for *auriculata.* An F_5 light pink *auriculata* derivative crossed with *macrophylla* (red *sessilifolia*) gave pink *sessilifolia* in F_1, and 133 pink *sessilifolia:* 40 pink *auriculata:* 53 red *sessilifolia:* 16 red *auriculata* in F_2, a very close approximation to an independent dihybrid expectation.

On the basis of these facts we have been bold enough to offer provisionally the following formulation for the major differences in leaf-base characters:

Ss, stenophylla versus *sessilifolia, SS* is long-petioled like *angustifolia, ss* broadly sessile like *macrophylla.* The heterozygote may possibly approach an intermediate condition similar to *latifolia.*

Ll, stenophylla versus *latifolia. SSLL* is long-petioled like *angustifolia;* and *SSll,* short-petioled like *latifolia,* and with a distinct but not broad wing on the petiole. *Latifolia* is evidently a modified petiolate form.

Aa, sessilifolia versus *auriculata, ssAA* has the broad clasping leaf-base characteristic of *macrophylla;* and *ssaa* the deeply constricted leaf-base with flaring auricles of *auriculata. Auriculata* is clearly a modified sessile form.

As to the completeness of dominance in any of these factor pairs, we can say very little because of the difficulty of evaluating the effect of the residual genotype. Likewise the significance of the wing in *latifolia* or of the auricles in *auriculata* is not definitely established on account of the extreme genetic difference which existed between the original parent varieties.

The Calycina-Virginica Series.—In the *calycina-virginica* (Maryland) series most of the attention was given to flower color and flower form. The flower color of *calycina* was red like that of *macrophylla,* and that of *virginica* was light pink like that of *angustifolia.* The results were in full agreement with those obtained from that series. The F_1 was pink and F_2 gave 73 pink: 23 red, with the same variation in the pink class as that noted for the preceding series. Five red F_2 segregants gave 125 F_3 plants all red-flowering. Of twelve F_3 families grown from pink segregants, three gave only pink-flowering descendants, and nine exhibited segregation into 3 pink: 1 red, the actual totals being 170 pink: 52 red.

Calycina is characterized by the production of split hose-in-hose flowers. The calyx is strongly developed and petaloid and it is also deciduous in contrast to the persistent and at times accrescent nature of the calyces of normal forms. This character proved to be a simple recessive. F_1 was normal except for slight suggestions of a petaloid condition of the calyx tips on some of the flowers of the F_1 plants. F_2 gave 61 normal: 35 split hose-in-hose. In F_3, seven families from F_2 split hose-in-hose segregants gave 175 plants all bearing split hose-in-hose flowers. Of ten families from normal F_2 segregants two gave only normal descendants, while eight exhibited segregation into normal and hose-in-hose in the numbers 133 normal: 42 split hose-in-hose. Four F_2 families were examined for simultaneous segregation of pink versus red and normal versus split hose-in-hose. The results were 109 pink normal: 36 pink hose-in-hose: 43 red normal: 11 red hose-in-hose, which is in substantial agreement with a 9 : 3 : 3 : 1 ratio for independent segregation in these two pairs of allelomorphs. The results establish the existence of a single pair of allelomorphs, *Cc*, for the character contrast normal versus split hose-in-hose (calycine) flowers.

The Alba-Macrophylla Series.—In the *alba* (White)-*macrophylla* series our attention was largely confined to flower color, *alba* being white and *macrophylla*, as we have seen, red. The F_1 in this case was definitely pink, and F_2 gave (combining 1911 and 1916 results) 180 pink: 58 red: 83 white. This result is in very satisfactory agreement with a 9 pink: 3 red: 4 white ratio, which may be accounted for by adding to the *Rr* pair of allelomorphs previously demonstrated a second pair, *Ww*, for colored versus white flowers. *Alba* is then *RRww*, and *macrophylla*, *rrWW;* and the F_1, *RrWw*, is pink as in the two previous series. Of five F_3 families grown from red F_2 segregants, three (*rrWW*) bred true for red; one (*rrWw*) gave 35 red: 14 white; and one gave the anomalous segregation product of 2 red: 23 white. Seven families were grown from pink F_2 plants. Five (*RrWw*) segregated for pink, red, and white in the numbers 73 pink: 25 red: 28 white; one (*RrWW*) gave 22 red: 3 pink; and one (*RRWw*) gave 33 pink: 9 white. Only one pink genotype, *RRWW*, was not demonstrated, but this is not inexplicable in view of the fact that only one in nine of the F_2 pink-flowering plants should belong to this genotype. Seven F_3 families were grown from white F_2 segregants. Among 191 plants, otherwise white-flowering, there was a single pink-flowering individual. It was doubtless a stray of some sort. The difference between the red flowers of *macrophylla* and the white ones of *alba*, therefore, finds a satisfactory formulation as a bigenic contrast.

Discussion of Results.—The results of the flower color studies set forth above appear at first sight to conflict with those which have been published by Allard.[4] He found that carmine, a color only slightly different from the red of *macrophylla*, was a simple dominant to pink; and when he crossed it with white, he obtained F_1 lighter than carmine, and an F_2 progeny which might have been interpreted as 9 carmine: 3 pink: 4 white. Certain back crosses which he made and out crosses of extracted whites to pink bear out this analysis. Of his varieties his pink (Maryland Mammoth) appears to be identical with our *virginica* (Maryland), consequently we are forced to assume that his carmine is genetically distinct from our red. It follows that if we add to the two pairs of factors for flower color which we have demonstrated, a third, *Pp*, for carmine dominant versus pink recessive, his results are brought into accord with ours. Certain experimental results which we have just secured and which we are reserving for future treatment demonstrate the correctness of this suggestion.

A general result of these investigations has been a demonstration of the complexity of difference from a genetic standpoint between any two of these so-called fundamental varieties of *Tabacum*. In one sense this result confirms the opinion of Comes and of Anastasia as to the manner of origin of the vast assemblage of *Tabacum* varieties. It goes further, however, and demonstrates the futility of seeking to determine affinities on the basis of morphological studies unaccompanied by experimental investigations. Thus, for example, we have seen such puzzling segregation products as the *auriculata* and *loriifolia* leaf types, the former with its peculiarly constricted leaf base, the latter with a much narrower leaf blade than either parent, coming out of the *angustifolia-macrophylla* series. Moreover, the demonstration of the existence of genetically distinct red-flowering varieties is another evidence of the limitations of purely morphological studies and of the errors in the determination of affinities to which such studies are subject. The genetic studies outlined above indicate merely that *Tabacum* is a group species like corn, barley, oats, etc., possessing a complex series of allelomorphic contrasts. The so-called fundamental varieties of *Tabacum* intercross freely and produce fully fertile progenies. They cannot genetically, therefore, be regarded as representing anything but a few very distinct genotypes. A demonstration that a few such varieties may contain within them the possibility by means of recombination of producing a host of secondary varieties does not really demonstrate that they are fundamental. In fact when we consider the fugitive nature of our *Tabacum* varieties, except in so far as they are kept isolated by natural or artificial means, the conclusion appears inevitable that we must regard all our varieties as fundamentally equivalent from a genetic standpoint. The really significant problem in considering the species is the determination of how these allelomorphic contrasts have come into existence. These investigations throw no light upon that problem.

We have been interested in the methodology of Mendelian analysis in *Tabacum*. Doubtless one of the reasons why our knowledge of the details of inheritance in *Tabacum* is so meager is because of the prevailingly quantitative or semi-quantitative nature of the character differences. Even in the case of flower color, the impression given by a series of varieties arranged in order of intensity from white to intense dark red is one of graduated differences in amount of a single pigment rather than in qualitatively different pigments. A definite alternative analysis can, however, be made even for these semi-quantitative characters by growing successive generations of segregating progenies until the progenies have been freed of segregation products other than those which it is desired to analyze. Furthermore, the establishment of constant derivative races and the subsequent study of intercrosses among them has been found to result in simplification of the difficulties of analysis. Both of these methods evidently depend upon stabilizing the residual genotype, which is a prime desideratum in the accurate analysis of semi-quantitative characters. The fact that such simplification of segregation can be accomplished and that semi-quantitative characters may then be subjected to analysis according to the qualitative mode of procedure argues not only for the adequacy of Mendelian principles in these cases, but for the identity in principle of qualitative and quantitative characters.

The experimental data cited above were obtained from cultures made possible by a portion of the Adams' Fund allotted to the Department of Botany by the Department of Agriculture of the University of California. The detailed account of this series of studies will appear in a forthcoming number of Vol. 5 of the University of California Publications in Botany under the title, Studies of inheritance in Nicotiana Tabacum, I. A report on the results of crossing certain varieties.

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[3] Setchell, W. A.: "Studies in *Nicotiana*, I," *Univ. Calif. Publ. Botany*, **5**, 1912 (1–88).

[4] Allard, H. A., "Some studies in blossom color inheritance in tobacco, with special reference to *N. sylvestris* and *N. Tabacum*," *Amer. Naturalist*, **53**, 1919 (79–84).

THE CORRELATION OF COMPOUND FORMATION, IONIZATION AND SOLUBILITY IN SOLUTIONS. OUTLINE OF A MODIFIED IONIZATION THEORY

BY JAMES KENDALL

CHEMISTRY DEPARTMENT, COLUMBIA UNIVERSITY*

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Introduction.—The anomaly of strong electrolytes has been a notoriously weak point in the ionization hypothesis ever since its inception. In fact, satisfactory agreement with the Ostwald dilution law (which follows from the application of the law of mass action to the ionization equilibrium $RX \rightleftharpoons R^+ + X^-$) has been definitely established only for two restricted types of electrolytes (weak acids and bases) in a single solvent (water) through a limited concentration range (dilutions greater than $N/16$).